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星叶草叶脉序的形态学及其系统学意义*

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THE MORPHOLOGY OF THE DICHOTOMOUS LEAF VENATION OF *CIRCAEASTER AGRESTIS* AND ITS SYSTEMATIC IMPLICATION

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Abstract Observations on the dichotomous leaf venation of *Circaeaster agrestis* found no intermediate forms of the fusion of vascular bundles between the two completely fused commissural veins of anastomoses and the two separate approximate veins, but found different degrees of the vestige of commissural veins . The fact indicates the impossibility of the formation of anastomoses from approximate veins. The occurrence of blind veins is related to the degeneration of teeth, the interruption of the commissural veins and the interruption of non-anastomosous veins at the branching point . Therefore, we considered the dichotomous leaf venation of this species as a reduced characteristic.

Key words *Circaeaster agrestis*; Venation; Anastomosis; Blind vein; Morphology

The leaf venation of *Circaeaster agrestis* Maxim. , like that of *Kingdonia uniflora* , is open dichotomous. Foster(1971, 1970, 1968, 1966, 1963) studied the leaf venation of *Circaeaster agrestis*, in which the anastomosis was found(Foster, 1963). He considered that the anastomosis was a parallel evolution of the similar characteristic occurring in the dichotomous venation of many ferns and gymnosperms, and formed from the approximate veins (Foster, 1968). These conclusions led to the consideration of *Circaeaster agrestis* as a representative of primitive angiosperms. The dichotomous leaf venation of *Kingdonia uniflora*

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was morphologically studied and regarded as a reduced characteristic by the present authors (Ren & Hu, 1996). Dose the same tendency occur in the leaf venation of *Circaeaster agrestis*? This is what we attempt to discuss in the present paper.

1 Materials and Methods

11050 pieces of leaves from 1500 individuals used in the present studies were collected from more than 10 populations in Taibai Mountains, Shaanxi Province from June to August in 1994 and 1995. They were fixed in FAA. The leaves with anastomoses and blind veins were stained with safranin. After being photographed, the leaves were embedded in paraffin wax, sectioned at 10 μm, and stained in saematoxylin and counter-stained with safranin. Some of the leaves were cleared in 5% NaOH, stained with safranin and made into permanent mounts.

2 Observations

The open dichotomous leaf venation of *Circaeaster agrestis* is formed by 2～5 times of repeated forking of the vascular bundle from the petiole, and each of the ultimate branches enters a distal marginal tooth (Plate 1:1). The following are the variations of the veins.

2.1 Anastomosis

An anastomosis means that two neighbouring veins which are named commissural veins approach each other and fuse into one. In the process of fusion, the two vascular bundles of the veins fuse completely to form a closed areola(Plate 1:2～19, 22). The anastomoses vary in the origin of commissural veins and the behaviour of fused veins. The commissural veins of an anastomosis may be daughter veins of the same order(Palte 1:2～4,7,12～14,16,17) or different orders of veins (Plate 1:5,6,8～11). They may also be the daughter veins of the same dichotomous vein(Plate 1:13) or different ones. In the latter case, the commissural veins may originate from two neighbouring daughter dichotomous veins whose mother veins are from the same (Plate 1:2～4,12,16,17)or different (Plate 1:5～7,9) dichotomous veins of higher order. The fused vein may enter a tooth directly(Plate 1:2～4,8,10,12,13, 16)or fork into two daughter veins, each of which enters a tooth(Plate 1:5,9), or one of them forks again into two daughter veinlets and each of them enters a tooth(Plate 1:7).

In some anastomoses, one of the two commissural veins is slender than the other or shows a tendency of reduction(Plate 1:10,11,14,15,17). Sometimes there are only 1～3 series of tracheary elements in the vascular bundle of commissural veins(Plate 1:18), or these tracheary elements are not connected with the other commissural vein(Plate 1:19). Sometimes one of the commissural veins is represented by only one or several tracheary elements extending towards the other(Plate 1:20,30～32) or from the opposite position (Plate 2:33), or by a vascular bundle without tracheary elements (Plate 1:21).

Among the leaves observed, 74 from 67 individuals have anastomoses. The number of the leaves with anastomosis in an individual is 1～3, and there is no more than one anastomosis in a leaf.

2.2 Approximate vein

The approximate veins are two closely neighbouring veins which seem to be one when observed by naked eyes or by magnifier(Plate 2:34,36). The observations under microscope with a series of cross or paradermal sections of the approximate veins show that their vascular bundles are separate (Plate 1:23, Plate 2:35,37,38).

2.3 Blind veins

Most of blind veins are upwards, which do not enter teeth at their distal ends. An upward blind vein usually occurs in lateral margins and is correspondent to an anomalous tooth (Plate 1:26～28; Plate 2:39～41). A normal tooth is subtriangular with a short arista at the apex, and the end of the ultimate veinlet terminates in the base of arista (Plate 1:24). The teeth may have different degrees of anomaly, sometimes the arista disappears (Plate 1: 25), or the tooth is semicircular (Plate 1:26,27)or wave-like(Plate 1:28; Plate 2:41); sometimes the blind end extends to the smooth leaf margin(Plate 2:42), or to the sinus between two neighbouring teeth(Plate 2: 43); sometimes the blind vein curves and its blind end extends to a neighbouring vein, which may indicate that the blind vein forms due to the interruption of a commissural vein (Plate 2:45); the extremely example is that the blind end is represented only by several tracheary elements(Plate 2:46). There is usually a segment of vascular bundle without tracheary elements at the blind end(Plate 1:28).

In the lateral margins of lamina, sometimes the two daughter veins of dichotomous veins are both blind (Plate 2:47). Usually the inner blind vein is longer and directs at a semicircular tooth, while the outer one at a wave-like tooth or the smooth leaf margin.

The downward blind vein enters a tooth at its distal end but is not connected with any vein at the base. The blind end does or does not approach a neighbouring vein, or sometimes it can be represented by a very short segment of vascular bundle below the tooth(Plate 2:48 ～50); sometimes one of the two daughter veins from a dichotomy does not have tracheary elements in the vascular bundle near the branching point(Plate 2:51). In a case, a vein is linked to a neighbouring vein at its distal end but is blind at the base(Plate 2:52).

If a vein has both distal and basal blind ends, it is an isolated vein (Plate 2:53～56). Sometimes the basal blind end curves and extends to a neighbouring vein(Plate 2:54). The isolated veins can occur in any region of a lamina.

Three cases of special blind veins were observed. A vein forks to form two daughter veins, one of which terminates in a tooth, while the other curves and then goes upwards parallel to the first vein, but becomes blind. On its curving point, another vein occurs and goes downwards blindly(Plate 2:57,58).

328 leaves from 251 individuals were found to have blind veins. The number of the leaves with blind veins is 1～6 per individual, and each leaf has 1～5 blind veins.

3 Discussion

The present authors do not agree with Foster who considered that the anastomoses in the dichotomous leaf venation of *Circaeaster agrestis* could form from the approximate veins (Foster, 1968). We did not find any intermediate forms of the fusion of vascular bundles between approximate veins and anastomoses, but did find different degrees of reduced commissural veins in anastomoses, e.g. the commissural veins become more slender than the neighbouring veins, or they are represented by the vascular bundle with or without 1~3 series of tracheary elements. The anastomoses may be reduced due to the interruption of the commissural veins at its distal or basal connecting point as shown in Plate 2:44,45,52, which makes an anastomosis open. Therefore, we suppose that the anastomosis in the leaf venation of *Circaeaster agrestis*, like that of *Kingdonia uniflora* (Ren & Hu, 1996) be a primitive characteristic compared to the open venation.

Blind veins, especially upwards blind veins in lateral margins, are correlated to the teeth degeneration. The sign of tooth degeneration is the disappearing of arista, then the tooth become obtuse, semicircular, wave-like in turn, and finally the smooth leaf margin forms. In the processes, the veins shorten and withdraw from the teeth to form blind vein. The occurrence of the blind dichotomous veins, in which the inner vein is longer and opposite a semicircular tooth, while the outer is shorter and opposite a wave-like tooth or the smooth leaf margin, showes obviously the relationship between the blind veins and the reduced teeth. Comparing the anastomoses shown in Plate 1:10,11, the blind veins shown in Plate 2:44, 45, 52 and the examples shown in Plate 2: 57,58 makes it obvious that some of the blind veins can form by the interruption of commissural veins. If an open vein has an interruption at its branching point and shortens, most of the downwards blind veins will form. Therefore, we do not agree with Foster's(1971, 1970) conclusions.

The above-metioned analyses show that the leaf venation of *Circaeaster agrestis* presents its reducing tendency both in vein structure and number. The tendency is consistent with other reducing characteristics of this species such as annual habit with little secondary growth in its root and hypocotyl(Ren & Hu, 1995), simplification of flower organs and disappearing of vascular bundle in sepels(Hu, *et al*., 1990).

The open dichotomous venation and anastomosis also occur in leaves of Cycadaceae and Ginkgoaceae(Foster & Giford Jr, 1974; Arnott, 1959; Troll, 1938). But in these gymnosperms, the anastomoses usually occur at the margins of pinna or lamina(Foster & Giford Jr, 1974), and no reduced tendency of commissural veins has been reported. The most important fact is that in these gymnosperms there are motile sperms which are as primary as those in ferns. Therefore, we come to the conclusion that it would be unsuitable to consider the open dichotomous leaf venation of *Circaeaster agrestis* as primary like that in gymnosperms, and that the systematic implication of the open dichotomous leaf venation of

Circaeaster agrestis was overemphasized in the past.

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Explaination of Plates

Plate 1 Leaf venation of *Circaeaster agrestis* 1. Venation without anastomosis and blind vein. ×2.5. 2～22. anastomoses. 2. ×2.5; 3. enlarged anastomosis shown in Plate 1:2. ×40; 4. ×3.5; 5. ×2.5; 6. enlarged anastomosis shown in Plate 1:5. ×40; 7～8. ×3; 9～10. ×2.5; 11. a commissural vein slender than other veins. ×40; 12～13. ×2.5; 14～15. enlarged areoles, showing the slenderized commissural veins. 14. ×30; 15. ×40; 16. ×2.5; 17. enlarged anastomosis shown in Plate 1:16. ×40; 18～21. degenerate commissural veins. 18. a commissural vein with 1～3 series of tracheary elements in vascular bundle. ×100; 19. a commissural vein interrupted at its distal end. ×100; 20. an end of tracheary element extending towards another vein. ×100; 21. vascular bundle of a commissural vein without tracheary element. ×100; 22a～22b. series of paradermal sections of an anastomosis, showing the fusion of vascular bundles of 2 commissural veins. ×110. 23a～23g. series of paradermal sections of an approximate vein. ×110. 24～28. variation of teeth. 24. a normal tooth. ×12; 25～28. anomalous teeth. 25. ×12; 26. ×12; 27. ×20; 28. ×20.

Plate 2 Leaf venation of *Circaeaster agrestis* 29～32. degenerate commissural veins. 29～30. an end of tracheary element extending towards another vein. ×120; 31. a commissural vein interrupted at its distal end. ×20; 32. a commissural vein with two ends of tracheary element extend at the opposite position. ×100. 33a～33b. enlarged veins shown in Plate 2:32. ×120. 34～38. approximate veins. 34. ×2.5; 35. enlarged approximate vein shown in Plate 2:34. ×40; 36. ×3; 37. enlarged approximate vein shown in Plate 2:36. ×30; 38. enlarged approximate vein. ×40. 39～58. blind veins. 39～46. upwards blind veins. 39～41. ×2.5; 42. a leaf with an upwards and a downwards blind vein. ×20; 43. ×2.5; 44～45. the blind veins seam to be formed from the interruption of a commissural vein. ×3; 46. an enlarged extremely shortened blind vein. ×120; 47. blind vein dichotomy. ×20; 48～52. downwards blind veins. 48. ×2.5; 49～50. very short blind veins below teeth. 49. ×30; 50. ×20; 51. a daughter vein(right) without tracheary elements in vascular bundle at the base. ×120; 52. same as Plate 2:44～45. ×30; 53～56. isolated

veins. ×2.5; 57~58. special blind veins. 57. ×2.5; 58. enlarged part of the curving region of a downward blind vein . ×120.

摘要 在星叶草叶二叉分枝脉序中,网结脉中2条完全汇合叶脉与靠近脉中完全分离叶脉间未发现任何形式的维管束汇合的中间类型,相反观察到了网结脉中不同程度的连接脉退化的痕迹,因此网结脉不可能由靠近脉形成;盲脉的出现与齿的退化、网结脉中连接脉的间断及非网结脉由分枝处间断等相关;上述事实表明星叶草叶的二叉分枝脉序应为一减化性状。

关键词 星叶草;脉序;网结脉;盲脉;形态学

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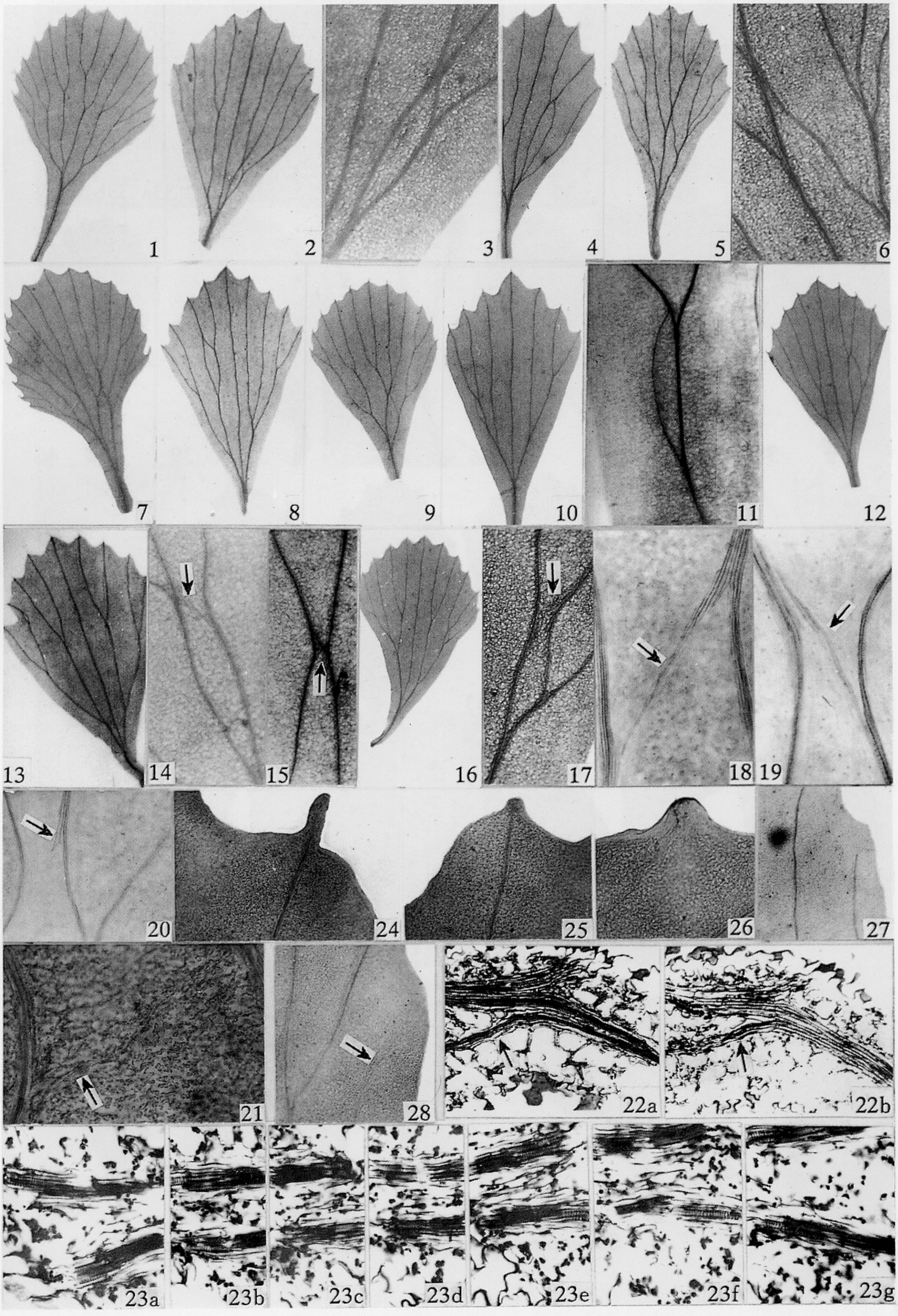
Ren Yi *et al*.: The Morphology of the Dichotomous Leaf Venation of *Circaeaster agrestis* and Its Systematic Implication　　Plate 1



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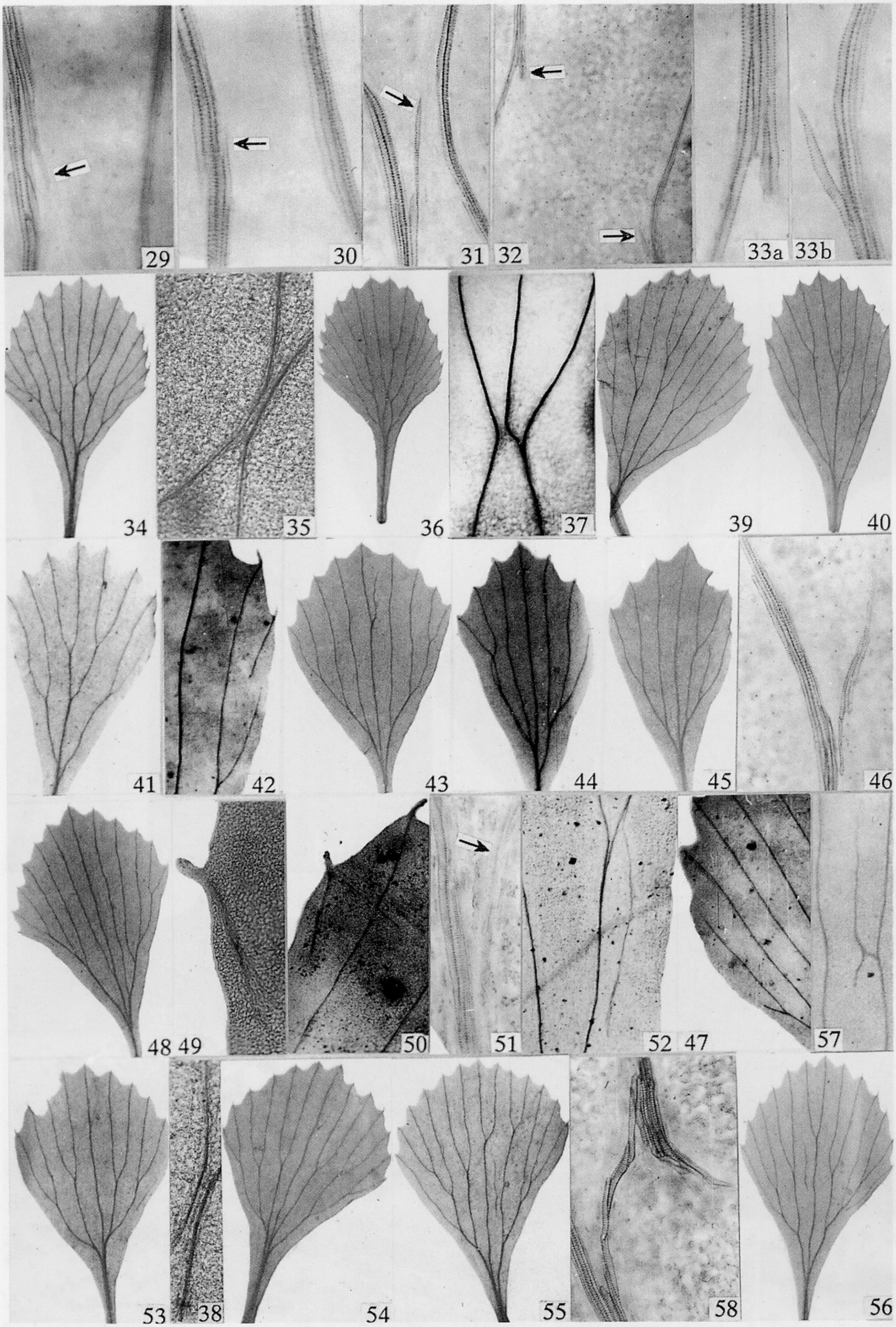

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